

Increase of a Caribbean leatherback turtle *Dermochelys coriacea* nesting population linked to long-term nest protection

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Abstract

The leatherback turtle *Dermochelys coriacea* is considered to be at serious risk of global extinction, despite ongoing conservation efforts. Intensive long-term monitoring of a leatherback nesting population on Sandy Point (St. Croix, US Virgin Islands) offers a unique opportunity to quantify basic population parameters and evaluate effectiveness of nesting beach conservation practices. We report a significant increase in the number of females nesting annually from ca. 18–30 in the 1980s to 186 in 2001, with a corresponding increase in annual hatchling production from ca. 2000 to over 49,000. We then analyzed resighting data from 1991 to 2001 with an open robust-design capture–mark–recapture model to estimate annual nester survival and adult abundance for this population. The expected annual survival probability was estimated at ca. 0.893 (95% CI: 0.87–0.92) and the population was estimated to be increasing ca. 13% pa since the early 1990s. Taken together with DNA fingerprinting that identify mother–daughter relations, our findings suggest that the increase in the size of the nesting population since 1991 was probably due to an aggressive program of beach protection and egg relocation initiated more than 20 years ago. Beach protection and egg relocation provide a simple and effective conservation strategy for this Northern Caribbean nesting population as long as adult survival at sea remains relatively high.
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1. Introduction

Population dynamics of the endangered leatherback *Dermochelys coriacea* turtle are poorly understood. Little information exists on basic parameters, such as age of maturity and survival probabilities, and this reflects the difficulty of obtaining reliable data from long-lived marine vertebrate populations with complex life histories (Chaloupka and Limpus, 2002). Reliable estimates of abundance and survival probabilities are needed for a better understanding of the demographic and ecologi-

cal processes that are relevant to long-term conservation programmes. These are best achieved for sea turtles through long-term studies at foraging grounds (Chaloupka and Limpus, 2001), but have not been possible for leatherbacks, which are inaccessible during most of the phases of their life-history due to their oceanic existence (Eckert, 2002). Population abundance and survival probability estimates are therefore based on capture–mark–recapture (CMR) studies of females that come ashore seasonally to nest.

The Virgin Islands Department of Planning and Natural Resources (VIDPNR) began flipper tagging in 1977 at the leatherback rookery on St. Croix (Fig. 1) and in 1981 initiated consistent beach monitoring each night

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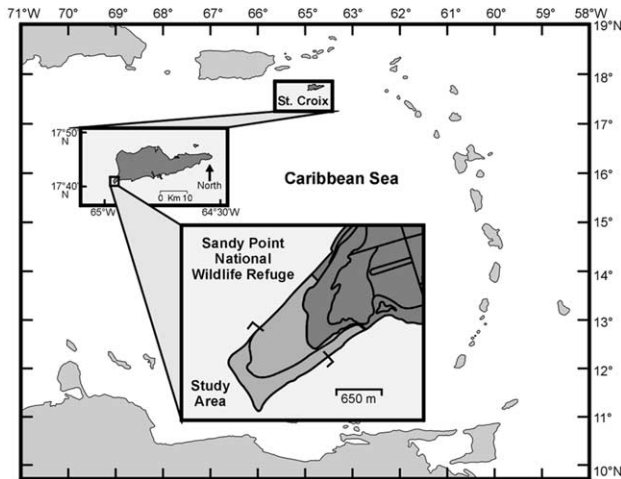


Fig. 1. Location of Sandy Point National Wildlife Refuge rookery on St. Croix (US Virgin Islands).

during the main part of the nesting season in order to survey the population, and to protect the nesters and their eggs (Boulon et al., 1996). This intensive monitoring has enabled every nester at this rookery to be tagged. However, the use of metal flipper tags for individual identification has been shown to be unreliable for leatherbacks (McDonald and Dutton, 1996; Rivalan et al., *in press*) and has led to the widespread assumption that survival of adult nesting females is low since tagged animals are rarely seen more than once (Boulon et al., 1996; Hughes, 1996; Dutton et al., 2001). The high flipper tag loss between nesting seasons (ca. 50% some seasons) prompted the use from 1985 of photo-identification as an additional capture–mark–recapture technique (McDonald et al., 1996), and then the use of Passive Integrated Transponder (PIT) tags from 1992 (Dutton and McDonald, 1994; McDonald and Dutton, 1996).

Despite this long-term tagging effort, poor flipper tag retention has prevented meaningful estimates of remigration and survival probabilities to be carried out with data prior to initiation of PIT tagging in 1992 (McDonald and Dutton, 1996). Here we analyze PIT tagging data from 1992 to 2001 to derive the first robust estimates of key demographic parameters for this northern Caribbean leatherback population, including survival and nesting probabilities as well as adult female abundance. We then use the trends in estimated nesting population abundance and hatchling production over a 20 year period (1982–2001) to evaluate the effectiveness of nest protection as a conservation tool.

2. Methods

2.1. Study site

Our study was based on a 3 km stretch of beach in the Sandy Point National Wildlife Refuge on St. Croix, US

Virgin Islands (Fig. 1; see Boulon et al., 1996). The data collection methods, which were described in Boulon et al. (1996) have been consistent from year to year. All the turtles that nest are usually encountered each night on this beach, since the population is relatively small, and the entire beach can be rapidly patrolled by foot. This has allowed a consistent monitoring program to be carried out for over 20 years with an intensity that has not been possible at other leatherback rookeries where the sheer numbers of turtles or the length of the nesting beach make it hard to encounter all the turtles nesting each night. A predictable annual pattern of sand erosion and deposition is the most serious natural threat to nests on this beach. In addition, leatherbacks often lay eggs at, or below the high water mark (HWM), and these clutches are washed away by the subsequent high tides (Mrosovsky, 1983; Whitmore and Dutton, 1985; Eckert, 1987). Nests laid in known erosion-prone areas, or below the HWM are considered to be “doomed” clutches, and a common management practice in many countries is to relocate them to hatcheries or stable beach areas (Dutton and Whitmore, 1983). At our study site on St. Croix, the percentage of nests considered doomed each season ranges from 25% to 68% (43% average) (McDonald-Dutton et al., 2001). Beginning in 1983, all these doomed clutches were relocated to stable areas immediately after laying. Eggs were reburied in hand-dug nests that resembled natural nests in shape and size (McDonald-Dutton et al., 2001). The location of each nest was recorded using triangulation to beach markers placed at 20 m intervals along the entire length of the beach. This allowed nests to be identified and monitored as described in Boulon et al. (1996).

2.2. Nester trend and hatchling production estimation

Each year hourly patrols were carried out from 20:00 to 05:00 h every night from April 1 until 10 days after the last nest was laid in August. During these patrols every leatherback encountered was tagged, nesting activity recorded, and if necessary, the “doomed” clutches were relocated (Boulon et al., 1996; McDonald-Dutton et al., 2001). During the rest of the year, and in particular during late February and March, daytime patrols were carried out to record any nesting activity. In years when nesting was observed prior to April, the beach was sporadically patrolled at night in order to identify the early nesters. We used a combination of metal flipper tags, photo-identification of the pineal spot (pink spot) and PIT tags to mark individuals (McDonald and Dutton, 1996). We analyzed photographic records from 1987 to 2001, and PIT tag records from 1992 to 2001 to identify remigrants, which are those leatherbacks that have nested at least once in a previous season. Prior to 1987, the numbers of remigrants reported were based solely on flipper tags. Beginning in 1992 nesters were

tagged with at least one PIT tag, and where possible, two PIT tags (one in each shoulder), as described in Dutton and McDonald (1994). These nesters were also tagged with a metal flipper tag on each rear flipper (McDonald-Dutton et al., 2001). A pink spot photograph was also taken each year a nester was encountered.

Each year a sample of nests was excavated soon after hatchlings emerged to calculate emergence success as: [(number of hatched shells-number of dead hatchlings in the nest)/total number eggs]. We then estimated annual hatchling production using a simple Monte Carlo simulation experiment (Vose, 1996) given the observed annual number of nests, expected annual clutch size and the expected annual emergence. Expected clutch size was drawn for each year from a Poisson probability mass function to reflect the distribution of the number of eggs per clutch recorded each year from the sampled nests. Expected emergence success (fraction of eggs in each sampled clutch that hatched and then also successfully emerged from the nest) was drawn from a beta probability density function to reflect the distribution of emergence success recorded each year from the sampled nests. The expected annual hatchling production was then estimated using 1000 Monte Carlo trials given the observed number of nests, Poisson distributed expected clutch size, and beta distributed hatchling emergence success for each year from 1982 to 2001. The Poisson mass function and the beta density functions were based on maximum likelihood fits to the data recorded for the sampled nests and were found to be appropriate sampling functions for the Monte Carlo experiment. Separate probability density functions for annual emergence success were used for the in situ clutches and the relocated (doomed) clutches because in situ clutches were observed to have slightly higher emergence success for all years from 1982 to 2001. Separate probability density functions for annual emergence success for each clutch class were also used for the 1997 and 1998 samples as these years were found to have significantly lower emergence success compared to all other years. The expected annual hatchling production was then derived from the 50th percentile (median) of the 1000 Monte Carlo trials for each year while uncertainty in these annual estimates was based on a 95% empirical percentile confidence interval using the 2.5th and 97.5th percentiles of the 1000 Monte Carlo trials for each of the 20 years (1982–2001). More details of the Monte Carlo simulation and sampling methods adopted here can be found in Vose (1996).

2.3. Survival, recapture and breeding probability estimation

We compiled the capture histories (CMR profiles) for 483 individual nesting females that were tagged

using PIT tags from 1992 to 2001. The primary sampling periods consist of the 10 years of the PIT tagging study with 9 fortnightly secondary sampling periods during each season within each primary sampling period – this comprises an open robust CMR sampling design (Kendall et al., 1997). The 2-week secondary periods within each year approximate the 9–12 day nesting cycle of female leatherbacks at the St. Croix rookery (Boulon et al., 1996). We then used an open robust design statistical modelling approach (Kendall and Bjorkland, 2001) to estimate the annual survival, recapture and breeding probabilities of the St. Croix nesters from the 483 CMR profiles. This open robust design statistical model accounts for temporary emigration or Markovian breeding behaviour due to skipped nesting seasons that is characteristic of sea turtle nesting populations, and enabled us to account explicitly for the skipped nesting behaviour of the Sandy Point leatherbacks. We fitted this model to the 483 CMR profiles using program ORDSURVIV (Kendall and Bjorkland, 2001). It is important to note that these models assume that the survival probability for nesters was the same as the survival probability for non-nesters in each sampling season (Kendall and Bjorkland, 2001).

2.4. Abundance estimation

We used a Horvitz–Thompson type estimator [$N_i = (n_i/(\rho_i^*(1 - \gamma_i)))$; see Seber, 1982] to derive annual adult female abundance estimates, where n_i is number of nesting leatherbacks captured at the Sandy Point rookery in the i th year, N_i is number of adult female leatherbacks (both nesters and non-nesters) in the sampled population in the i th year, ρ_i is estimated recapture probability in the i th year and γ_i is estimated non-nesting (non-breeding) probability in the i th year. Recall that the annual recapture (ρ_i) and non-nesting (γ_i) probabilities were derived from the open robust design model fitted to the 483 CMR profiles using program ORDSURVIV (Kendall and Bjorkland, 2001). Simpler forms of the HT estimator have been used previously for estimating sea turtle population abundance (Chaloupka and Limpus, 2001; Balazs and Chaloupka, 2004; Bjorndal et al., 2005). We estimated the long-term linear trend in the HT adult female leatherback abundance estimates using a linear regression model with first order moving average error [MA(1): Judge et al., 1985] to account for any temporal correlation. The response variable (HT annual abundance estimate) was in natural log form so that the parameter estimate for year (1994–2001) was interpretable as a constant annual population growth rate. This MA(1) linear regression model was implemented with program SHA-ZAM (White, 1997).

3. Results

3.1. Nester census and hatchling production estimation

The observed number of females nesting annually has increased significantly from ca. 18–30 in the early 1980s to 186 in 2001 (Fig. 2(a), Table 1). Estimated hatchling numbers increased from about 2500 in 1982 to nearly 50,000 in 2001 (Fig. 2(b)). There was minimal hatchling production prior to 1982, when we began relocating almost all of the “doomed” nests laid in erosion zones or below the HWM each season. The improved individual identification techniques have allowed us to reliably identify first-time nesters and distinguish remigrants. We have used photo-identification and PIT tags to identify ca. 33% of untagged (=no flipper tags) turtles as remigrants (Table 1). In general this is an indication of the extent to which flipper tagging underestimates the number of remigrants each year.

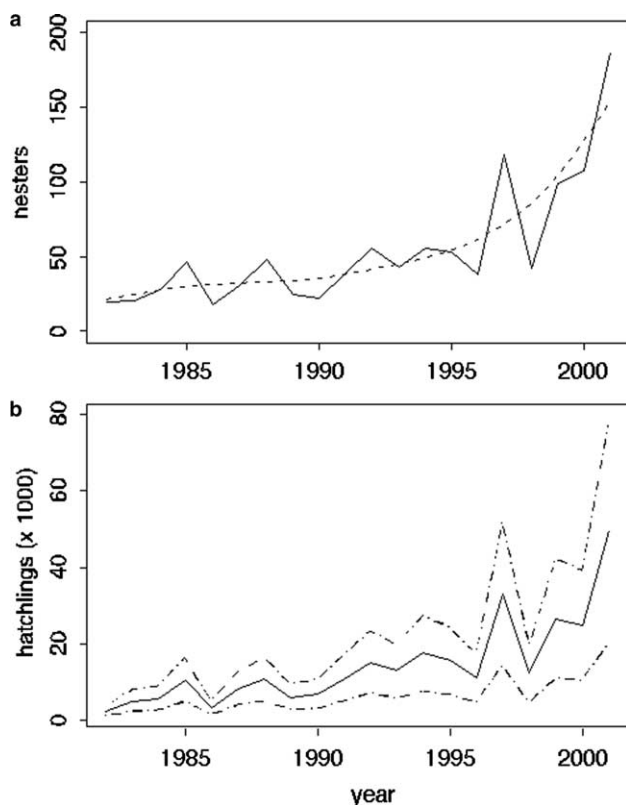


Fig. 2. Number of female leatherbacks nesting each year from 1982 to 2001 at the Sandy Point rookery shown in panel (a) by solid curve to highlight the underlying long-term trend in nesters shown by a robust cubic spline smooth (Hastie and Tibshirani, 1990) fitted to those data (dashed curve). Panel (b) shows the estimated annual hatchling production at the Sandy Point rookery since 1982 (solid curve = expected hatchling production derived from a simple Monte Carlo simulation experiment, dashed curves = 95% empirical percentile-based confidence bands derived from 1000 Monte Carlo trials for each year; see Section 2).

Since 1996, PIT tagging has replaced photo-identification as the primary tool for confirming remigrants among the nesters that have lost all flipper tags (Table 1). Nonetheless, photo-identification is still useful as an independent method to evaluate retention of PIT tags. While the longest remigration interval observed was 11 years, most remigrants returned to nest within 2–3 years (Fig. 3(a)). Only 3 turtles were observed to nest in two consecutive years. The most common remigration interval was 2 years (ca. 45% when corrected for survival, Fig. 3(b)).

3.2. Survival, recapture and breeding probability estimates

The most parsimonious model fitted to the 483 CMR profiles using ORDSURVIV (Kendall and Bjorkland, 2001) comprised (1) constant rookery arrival, detection and departure probabilities both within and among nesting seasons, (2) constant annual survival probability but (3) time-varying nesting (breeding) probabilities for females that have not nested in the previous year (first order Markovian breeding behaviour). This model fitted the 483 CMR profiles adequately ($\chi^2 = 573.2$, $df = 573$, $P = 0.49$) with high detection probability for the secondary samples (mean = 0.92, SE = 0.005). The mean annual survival probability was estimated as 0.893 (95% confidence interval: 0.87–0.92), which is consistent with other estimates for various sea turtle species (Chaloupka and Limpus, 2002; Bjorndal et al., 2003). The estimated annual nesting probabilities ($1 - \gamma_i$) ranged from 0.32 to 0.68, which is the proportion of adult females from the sampled population that nested in each year. The mean annual nesting probability was 0.46, which is equivalent to a remigration interval of ca. 2.2 years ($\sim 0.46^{-1}$) and so is consistent with the survival corrected estimate shown in Fig. 3(b).

3.3. Population abundance trend

The Horvitz–Thompson (HT) estimates of adult female abundance from 1994 to 2001 are shown in Fig. 4. It is doubtful that valid confidence intervals can be derived for these HT abundance estimates given the Markovian breeding behaviour due to skipped nesting seasons of the Sandy Point leatherbacks (see Fig. 3(a)). This annual breeding behaviour was nonetheless explicitly accounted for as the non-nesting probability (γ). This expected trend in the population, which comprises both the nesters and the non-nesting females, appears to have been increasing at ca. 13% pa (95% CI: 9–17%). The difference between the 2 curves in Fig. 4 reflects the proportion of adult females (dashed curve) that was observed to nest in each year (solid curve) at the Sandy Point rookery.

Table 1
Leatherback remigrations to Sandy Point from 1977 to 2001 (population not monitored 1978 and 1980)

Season	Total turtles encountered	Total remigrant	Migrants from Puerto Rico ^a	PIT tag only	Photo-ID only	Recruits (untagged turtles)
1977	10 ^b	0	N/A	N/A	N/A	N/A
1979	6 ^b	0	N/A	N/A	N/A	N/A
1981	20 ^c	3 ^d	N/A	N/A	N/A	N/A
1982	19	1 ^d	N/A	N/A	N/A	N/A
1983	20	9	N/A	N/A	N/A	11
1984	28	4	N/A	N/A	N/A	24
1985	46	16	N/A	N/A	N/A	30
1986	18	3	N/A	N/A	0	15
1987	29	16	N/A	N/A	2	13
1988	47	17	N/A	N/A	5	30
1989	24	7	N/A	N/A	1	17
1990	22	6	N/A	N/A	4	16
1991	39	16	N/A	N/A	4	13
1992	55	25	0	N/A	11	30
1993	43	17	0	0	7	26
1994	55	24	2	0	4	31
1995	53	28	1	0	0	25
1996	38	24	0	3	1	14
1997	118	57	3	0	0	61
1998	42	25	1	8	0	17
1999	99	50	1	8	0	49
2000	107	45	0	16	0	62
2001	186	96	6	43	0	90

^a Number of leatherbacks observed nesting each season on St. Croix that had nested originally on Culebra, Puerto Rico, the previous season.

^b Does not represent total number of turtles nesting.

^c May or may not represent total number of turtles nesting.

^d Not accurate due to incomplete tagging in previous years; proportions in later years are more accurate but still not complete.

4. Discussion

4.1. Abundance and survival probability estimates

The increase in the number of nesters we report here is consistent with the increasing trends documented on a more qualitative basis at other leatherback populations throughout the Caribbean (Spotila et al., 1996; Stewart and Johnson, 2003). The rapid growth rate (ca. 13% pa) that we estimated for the St. Croix leatherback population based on our robust CMR study is similar to those documented for increasing populations in other species of sea turtles (Bjorndal et al., 1999; Peñaflores et al., 2000; Balazs and Chaloupka, 2004; Troëng and Rankin, 2005). The increasing trend described here for Caribbean leatherbacks contrasts sharply with the dramatic declines of nesting populations in the Pacific (Chan and Liew, 1996; Spotila et al., 2000; Sarti et al., 1996), and with the listing of leatherbacks as Critically Endangered worldwide in the World Conservation Union (IUCN) Red List (<http://www.redlist.org>).

The estimated annual survival probability for the nesting females was high at ca. 0.893 (95% CI: 0.87–0.92). This is the first reliable estimate of adult survival for leatherbacks, and given that the population is increasing rapidly, this provides a sound minimum estimate of natural adult survival probability for use in future demographic simulation models (Chaloupka, 2002).

Moreover, the survival probability estimate is likely conservative, since some of the turtles may have permanently emigrated to other rookeries where they remain unreported. Individual leatherbacks are known to occasionally nest on different beaches in different years, and even during the same nesting season (Eckert et al., 1989; McDonald-Dutton et al., 2001). Between 1994 and 2001 at least 14 turtles that nested on St. Croix were remigrants originally tagged on the neighboring island of Culebra, Puerto Rico (Table 1). Other tag returns have been reported from Vieques, mainland Puerto Rico, British Virgin Islands, Anguilla (Boulon et al., 1996); and Dominica (W. Coles, personal communication).

Given that tagging and monitoring has not been carried out on the many small beaches and islands in the region around St. Croix, these tag returns appear to underestimate the regional interchange suggested by the estimated abundances from our study, and suggest that the St. Croix population is one component of a regional stock that includes other nesting beaches in neighboring Puerto Rican islands, British Virgin Islands, and possibly others in the Antilles. An expanded CMR study comprising concurrent monitoring at several leatherback rookeries in the Caribbean and using multi-strata estimators (Brownie et al., 1993) is needed to resolve whether there is local dispersal and what affect such behaviour might have on estimation of leatherback survival for a specific nesting population. Just such a multi-strata

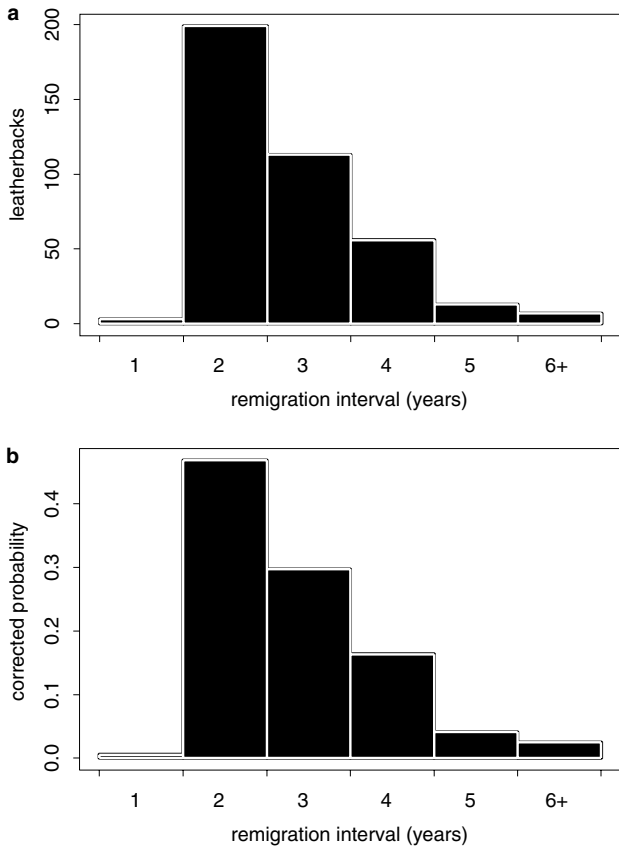


Fig. 3. Panel (a) shows the frequency distribution of the remigration intervals (years between consecutive nesting seasons) recorded for leatherbacks nesting at the Sandy Point rookery. Panel (b) shows the probability of the remigration interval frequencies shown in (a) but also corrected for annual survival given the number of years since the previous nesting. Annual survival probability was derived using an open robust design capture–mark–recapture model for the leatherback nesters recorded over the 11 year sampling period from 1991 to 2001 (see Section 2).

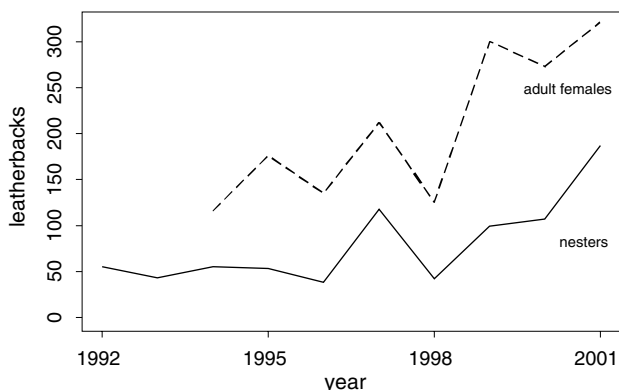


Fig. 4. Trend in estimated adult female population abundance. Dashed curve shows the Horvitz–Thompson type estimate of adult females in the population that nests at the Sandy Point rookery conditioned on annual recapture and nesting probabilities (see Section 2). Estimates only available from 1994 as the annual nesting probabilities in the open-robust design model are only estimable from 1994 onwards. Solid curve shows the number of nesters recorded at the Sandy Point rookery over a similar sampling period for comparison (see also Fig. 2(a)).

CMR study of Roseate Terns not only found significant spatial variation in adult survival but also provided important insights into regional dispersal dynamics within a seabird metapopulation (Spendelov et al., 1995).

4.2. Evaluation of conservation measures

The significant St. Croix leatherback population increase (Figs. 2 and 4) could be the result of improved adult survival and/or an increase in recruitment resulting from either improved hatchling production or oceanic juvenile survival. Our estimates of nester survival probabilities were constant for the 10-year period of our study, indicating that improved adult survival (at least for nesters) does not explain the recent increase of the St. Croix population. Also there is no evidence so far for any recent increase in oceanic juvenile survival. We believe that the exponential growth in the observed adult numbers beginning in 1991–1992 (Fig. 2(a)) is the result of the order of magnitude increase in hatchling production that began in 1982 (Fig. 2(b)), which indicates a lag of ca. 12–14 years before the onset of the increase in the adult nesting population. These trends are consistent with the average age of maturity of 9–15 years that has been proposed for leatherbacks (Zug and Parham, 1996).

While it has not been possible to conduct hatchling tagging experiments to directly determine growth and age of maturity, or whether hatchlings produced on St. Croix return as adults to nest on their natal beaches, the improved identification techniques since 1992 have allowed us to reliably distinguish between remigrants and first-time nesters (McDonald and Dutton, 1996). This information on nesting history, when combined with genetic data, allows us to infer family relationships among closely related females (Dutton et al., 2002). We have begun to construct DNA fingerprints based on data from an array of microsatellite markers (Dutton et al., 2003) as part of an extensive study that includes almost all the leatherbacks that have nested on St. Croix since 1992, and have found close family relations among the 37 nesters that have been analyzed to date (Fig. 5). Although the genetic data by themselves do not allow distinction between mother–daughter relations and full siblings, we have found at least two cases where one of the first order relatives was a remigrant that had been tagged in the early 1980s and therefore likely to be the mother of the recent first-time nester (Fig. 5).

These recent genetic results based on DNA fingerprinting (Fig. 5) provide compelling new evidence that some first-time nesters are indeed the offspring of nesting leatherbacks that were protected in the earlier years. This is consistent with indirect evidence of natal homing in St. Croix leatherbacks previously reported from population genetic studies (Dutton et al., 1999; Dutton

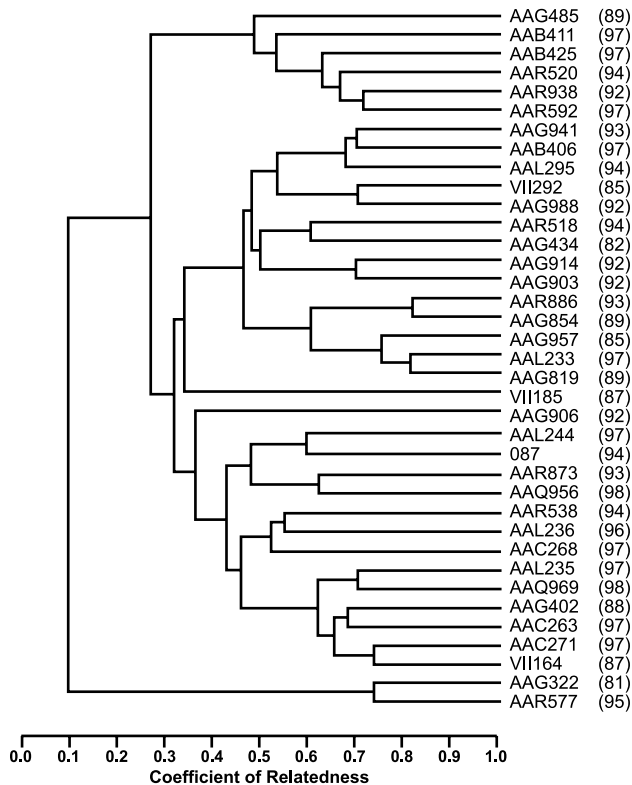


Fig. 5. Family groups identified among leatherbacks in the St. Croix rookery. The coefficient of relatedness (Queller and Goodnight, 1989) between 37 nesters was calculated from genetic data from 9 microsatellite loci (Dutton, 2002; Dutton et al., 2002), using RELATEDNESS 5.0 (<http://gsoft.smu.edu/Gsoft.html>). $R \geq 0.5$ indicates first order relatives (e.g., mother–daughter or full siblings). $R \geq 0.25$ indicates second order relatives (e.g., cousins). Individuals in each of the groups of first order relatives shown also shared the same mtDNA haplotype (Dutton et al., 1999) confirming connection through female lineages, since mtDNA is inherited maternally. The year the turtle was first observed to nest is given in brackets; old-timers, such as AAG322 (identified in 1981) and AAG434 (identified in 1982) are most likely mothers of recent (post 1993) first-time nesters such as AAR577 (1995), and AAR518 (1994), respectively.

et al., 2003), and reinforces our conclusion that the population increase we report here is at least in part the result of conservation measures initiated on St. Croix over 20 years ago. Further work is needed to define the structure and geographic boundaries of the regional metapopulation, and to assess whether the enhanced hatchling production resulting from conservation measures on St. Croix has contributed to the leatherback population increases that have been observed recently in the small rookeries in neighbouring islands and elsewhere around the wider Caribbean. While leatherback rookeries in the St. Croix – Puerto Rico – Antilles metapopulation probably benefited from enhanced hatchling production on St. Croix, as well as some beach protection of their own, other factors, such as favourable oceanic conditions for juvenile survival and growth, may be important and warrant further research.

4.3. Conclusions

The relatively high annual nester survival probability estimated in this study suggests that adult females are more resilient than previously believed to the hazards leatherbacks face at sea, as evidenced by the many turtles that we have seen returning repeatedly to nest on St. Croix despite open wounds, scars from entanglement in fishing gear and other marine debris, and longline hooks embedded in their flippers. The impacts of incidental take of leatherbacks in pelagic and coastal fisheries are of grave concern and largely unknown. Insights into some of the basic demographic parameters from this study will help with modelling efforts to evaluate the potential impacts of these sorts of fisheries. It is important to continue intensive tagging on St. Croix in order to enable detection of changes in estimated annual nester survival probabilities that might signal changes in the magnitude, or the appearance of new at-sea impacts. This study illustrates the value of long-term, consistent monitoring and conservation programmes both in terms of direct recovery of endangered and threatened species, and research that can be applied to informed management policies. We have demonstrated that a relatively simple and inexpensive management intervention (beach protection and egg relocation) can be an effective tool for increasing leatherback populations if applied over a sufficiently long period of time. However, conservation measures implemented solely on the nesting beaches may not be effective when in-water mortality levels are higher than those we found for St. Croix nesters. For example, high adult mortality from coastal fisheries may have rendered egg protection measures at the rookery in Terengganu, Malaysia ineffective (Chan et al., 1988). Likewise, if the anthropogenic and environmental factors impacting survival at sea are more significant in the eastern Pacific than in the Atlantic, then egg protection alone may be insufficient to reverse the severe declines that have occurred in the eastern Pacific leatherback rookeries in Mexico and Costa Rica (Spotila et al., 2000; Sarti et al., 1996). Nevertheless, the beach protection measures we have described are a necessary component of any strategy to recover depleted leatherback populations in the long run.

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